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The scolopidial accessory organ in *Gonatoxia* bush-crickets (Tettigonioidea, Phaneropterinae, Holochlorini)

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Abstract

The scolopidial accessory organ is a relatively small and compact chordotonal organ consisting of mechanosensory scolopidial sensilla. The accessory organ is placed in the tibia next to the larger subgenual organ in several Orthoptera. In other orthopteroid insects, the accessory organ detects substrate vibrations in low frequency ranges. Among Tettigonioidea katydids or bush-crickets, the accessory organ has been described so far in only a few species. The peripheral nerve pattern for the two chordotonal organs usually includes two separate nerve branches for each sensory organ. Within the Phaneropterinae (leaf katydids or sickle-bearing bush-crickets), some differences occur as the accessory organ can share a single nerve branch with the subgenual organ. Here, the accessory organ in two phaneropterine species of the East African genus *Gonatoxia*, *G. immaculata* Karsch, 1889, and *G. helleri* Hemp, 2016, is investigated. The aim is to document the accessory organ and its nerve pattern for further tettigonioid species and to provide a first report for species from the Holochlorini. The accessory organ was present in both species in all leg pairs. The number of sensilla was 5–12. The sensillum numbers were slightly lower in *G. helleri* than in *G. immaculata*. The accessory organ has a nerve branch that is separate from the nerve branch for the posterior subgenual organ. This neuroanatomy, including the nerve pattern, is similar to most other tettigonioids. The findings support the occurrence of the accessory organ among the different subgroups of Phaneropterinae, and in Tettigonioidea at large, and raise the possibility of behaviorally relevant vibrational inputs.

Keywords

Biotremology, chordotonal organ, mechanoreception, neuroanatomy, Orthoptera, sensory physiology

Introduction

Orthoptera, including Tettigonioidea (katydids or bush-crickets), detect different mechanical stimuli such as sound, substrate vibrations, or body posture by mechanosensory organs located in the legs. The subgenual organ complex is of particular interest for the detection of airborne sound and substrate vibrations, having a few separate chordotonal organs with their sensilla in different groups and locations in the proximal tibia. The subgenual organ is an important receptor organ for substrate vibrations found in all Orthoptera (e.g., Strauß et al. 2021). The highest number of different sensory organs in the subgenual organ complex are found in Ensifera, including the Tettigonioidea, with up to four chordotonal organs (Strauß et al. 2021). This complex of mechanosensory organs occurs in all leg pairs. In Tettigonioidea, a tympanal hearing organ is differentiated only in the prothoracic legs (Friedrich 1927, Houtermans and Schumacher 1974, Lakes and Schikorski 1990, Lin et al. 1994, Stumpner and Nowotny 2014).

The complex acoustic communication of the Tettigonioidea has been well studied (Gerhardt and Huber 2002, Greenfield 2016, Song et al. 2020, Hall and Robinson 2021). Acoustic signals are species-specific and have been analyzed in numerous species of Phaneropterinae—the leaf katydids, bush katydids, and sickle-bearing bush-crickets—with males and females frequently exchanging signals in acoustic duets in this group (Heller 1990, 2006, Heller and von Helversen 1986, Heller et al. 2015). Airborne sounds are typically perceived by the tympanal hearing organs. Another chordotonal organ in the tibia is the accessory organ (or German "Nebenorgan"), which is located at the posterior side of the tibia and close to the subgenual organ (see Strauß 2017 for a review on the accessory organ). It is found in several orthopteroid groups, such as cockroaches and heel walkers, and in certain ensiferan taxa, such as Rhaphidophoridae and Tettigoniidae (Strauß 2017, 2018). The accessory organ is relatively small with an average of 5–15 scolopidial sensilla. It is located closely and under the leg cuticle, and the sensilla are likely tuned to low-frequency vibration stimuli transmitted over the leg cuticle (in the range of 50–300 Hz; Schnorbus 1971, Strauß 2017, Stritih-Peljhan et al. 2019). In

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Tettigonioidea, the subgenual organ is larger than the accessory organ (Lakes-Harlan and Strauß 2014, Strauß 2017). The accessory organ has been described for eight tettigonioid species (Schwabe 1906, Strauß et al. 2016), but the distribution of the accessory organ in this group is not resolved. Some variation has been seen in the nerve pattern among the Phaneropterinae. Usually, the subgenual organ and accessory organ have separate nerve branches in the tibia, but in *Poecilimon ornatus* (Schmidt, 1850) (in Haidinger 1850), they share a single nerve branch (Strauß et al. 2016).

The Phaneropterinae is the largest subfamily in Tettigonioidea (Ingrisch and Rentz 2009, Heller et al. 2015, Mugleston et al. 2018). Thus, the different subgroups of Phaneropterinae allow for comparisons of the occurrence of the chordotonal organs and their homogenous or divergent neuroanatomy, including the accessory organ and its nerve pattern. Hence, to further sample the distribution and neuroanatomy of the accessory organ for Phaneropterinae, we investigated two species from the East African genus *Gonatoxia* Karsch, 1889 as representatives of the phaneropterine tribe Holochlorini (Hemp et al. 2016, Cigliano et al. 2025). Their examination provided neuroanatomical data for an additional and previously unstudied tribe. The genus *Gonatoxia* was recently taxonomically revised (Hemp et al. 2016), and the monophyletic group contains five species (Warchałowska-Śliwa et al. 2021). Like other Phaneropterinae, *Gonatoxia* produce acoustic signals for mate localization and pair formation through tegminal stridulation (Hemp et al. 2016, Heller and Hemp 2017). *Gonatoxia* species have been studied for their acoustic signals (Hemp et al. 2016, Heller and Hemp 2017), the diversity and evolution of karyotypes (Hemp et al. 2016, Warchałowska-Śliwa et al. 2020, 2021), and their phylogenetic relationships (Warchałowska-Śliwa et al. 2021).

For this study, we compared the occurrence of the accessory organ, the number of sensilla, and the innervation of the subgenual organ and accessory organ in *Gonatoxia immaculata* Karsch, 1889 and *Gonatoxia helleri* Hemp, 2016 (Hemp et al. 2016) to those of other Phaneropterinae. Axonal tracing was used to document the sensilla of the accessory organ and the nerve pattern of the accessory organ and subgenual organ. These data contribute to a broader sampling of the mechanosensory organs in Tettigonioidea and to the diversity of the subgenual organ complex in orthopteroid insects. The neuroanatomy of the accessory organ in other Tettigonioidea species suggests that the accessory organ is also present in *Gonatoxia* species. We expect to find a neuroanatomical organization similar to that in other Phaneropterinae, including in the number of scolopidial sensilla and the nerve pattern of the accessory organ.

Materials and methods

Insects.—*G. immaculata* (Fig. 1) and *G. helleri* reside in Tanzania (Hemp et al. 2016). In this study, 9 *Gonatoxia immaculata*—six females and three males (raised from eggs in the laboratory)—and 5 *Gonatoxia helleri*—two females and three males (one F1-generation male raised in the laboratory and two females and two males collected in Mazumbai, Usambara Mountains, Tanzania in May 2021)—were examined.

The data for *G. immaculata* included here were obtained from 24 legs (9 prothoracic legs, 9 mesothoracic legs, 6 metathoracic legs), and for *G. helleri*, from 12 legs (5 prothoracic legs, 6 mesothoracic legs, 1 metathoracic leg). The experiments documented in this study complied with the principles of animal care of the

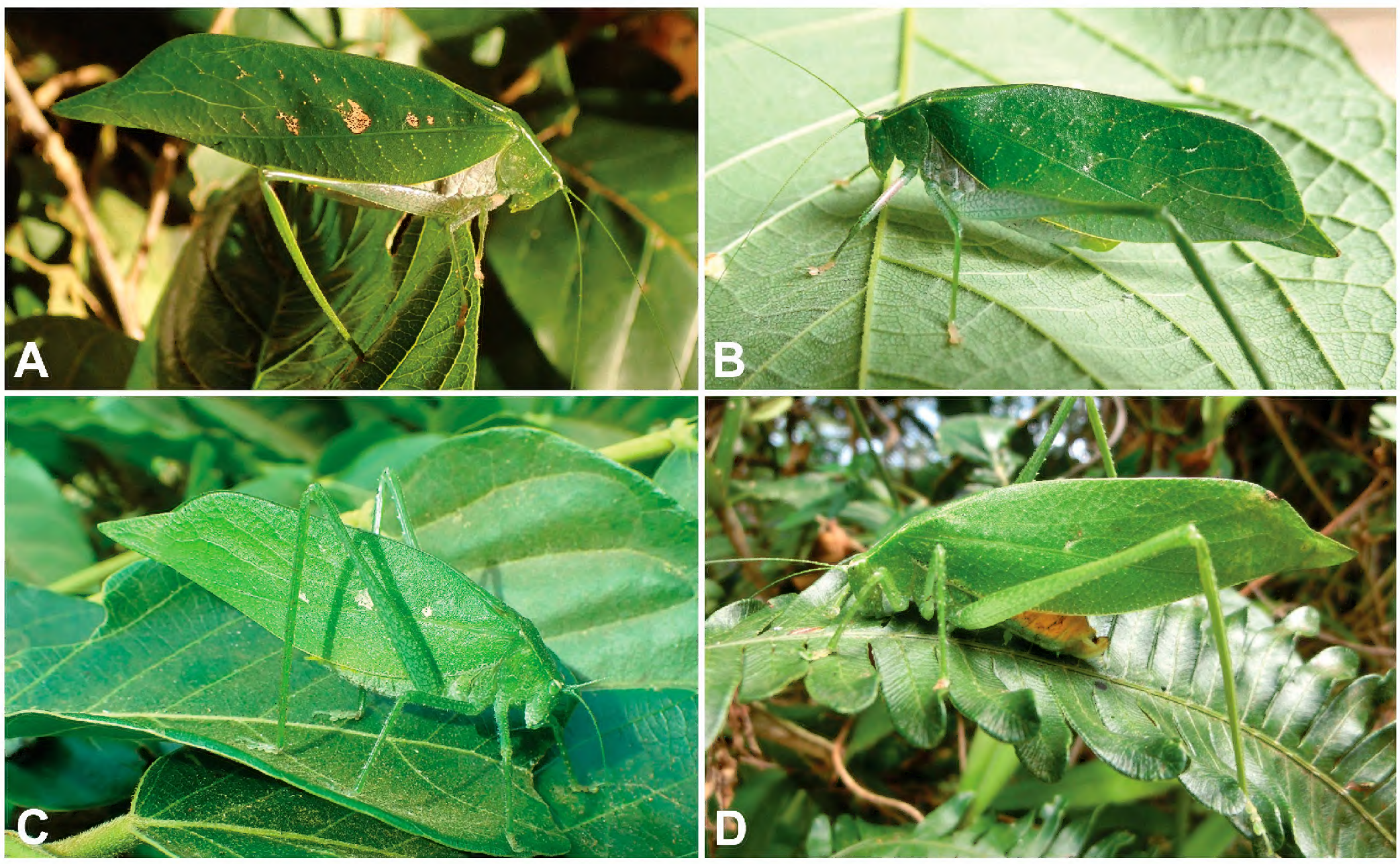

Fig. 1. Individuals of *Gonatoxia immaculata* (top) and *Gonatoxia helleri* (bottom). **A, C.** Male individuals; **B, D.** Female individuals. Individuals of both species measure 5.0–5.5 cm from the head to the tip of the wings.

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Neuroanatomy.—The neuroanatomy was investigated by retrograde axonal tracing applying 5% solution of cobalt chloride ($CoCl_2 \times 6\ H_2O$, Merck, Darmstadt, Germany) dissolved in *aqua dest* (see Altman and Tyrer 1980). The preparation followed the procedure described by Strauß et al. (2012) on isolated legs of bush-crickets. Before dissection, the insects were briefly cold-anesthetized at 4 °C for 10 min. The femur of Tettigonioidea contains two main nerves, the tympanal nerve (N5B1) and the leg nerve (N5B2) (Schumacher 1973, Lakes and Schikorski 1990); N5B2 contains the axons from the accessory organ and posterior subgenual organ (Strauß et al. 2016). After cutting the two nerves in the femur with iridectomy scissors, axonal tracing was applied by placing the nerves in a glass capillary filled with cobalt solution. After incubation at 4 °C for 48 hours, the cobalt was precipitated by incubation with 1% ammonium sulphide solution (Alpha Aesar, Karlsruhe, Germany) (in locust saline, pH = 7.4; Clements and May 1974) for 15 min. The legs were rinsed twice in locust saline, fixed in 4% paraformaldehyde (Sigma-Aldrich, St. Louis MO, USA) dissolved in phosphate buffer (0.04 mol/l Na_2HPO_4, 0.00574 mol/l $NaH_2PO_4 \times 2\ H_2O$; pH = 7.4) for 60 mins, dehydrated in a graded ethanol series (Carl Roth, Karlsruhe, Germany), and finally cleared in methyl salicylate (Merck, Darmstadt, Germany).

Microscopy and documentation—Each leg was mounted on a microscopy slide in methyl salicylate and viewed on an Olympus BH-2 microscope (Olympus, Shinjuku, Japan). Digital photographs were taken with a Leica DFC 7000 T digital camera (Leica Microsystems CMS GmbH, Wetzlar, Germany) (1920 × 1440 pixels) via the Leica Application Suite version 4.9. Series of micrographs were taken from some preparations, and these series were stacked using the freeware program CombineZP (Alan Hadley; https://www.hadleyweb.pwp.blueyonder.co.uk).

The nerve pattern in the proximal tibia was drawn using a Leitz Dialux microscope (Leitz, Wetzlar, Germany) with a drawing attachment (Leitz) and digitally redrawn in CorelDraw 11 (Corel, Ottawa, Canada).

Statistics.—Statistical analysis of the numbers of sensilla in the accessory organ of *G. immaculata* included the Kolmogorov–Smirnov normality test and ANOVA using GraphPad Prism 4 (GraphPad, San Diego, CA, USA).

Neuroanatomy and nomenclature of nerves.—The nomenclature of the nerves in the tibia (N5B1, N5B2) is used as established for Tettigonioidea (Campbell 1961, Lakes and Schikorski 1990). The nerve branches from the main nerves in the tibia of first and second order are numbered from proximal to distal (T1, T11) (Strauß et al. 2016).

Results

The accessory organ was present at the posterior tibia of all leg pairs of *G. immaculata* and *G. helleri*, and it was innervated by nerve N5B2, the major leg nerve. It was located close to the posterior part of the subgenual organ (Figs 2, 3A–C). The position of the accessory organ and the nerve pattern are identical in both species (but see below for differences in sensillum numbers). In the following, data are shown for *G. immaculata*, for which more preparations were obtained. However, the findings apply to both species. The accessory organ was associated with a single posterior campaniform sensillum (a mechanosensillum detecting cuticle strain), and further campaniform sensilla were placed on the proximal and dorsal tibia (Fig. 2). The nerve pattern was identical between the prothoracic legs (Fig. 2A), mesothoracic legs (Fig. 2B), and metathoracic legs (Fig. 2C). Nerve N5B2 is associated with the accessory organ and the posterior subgenual organ by distinct nerve branches for each chordotonal organ from a common branch, N5B2-T12 (Fig. 2).

The accessory organ was similar in neuroanatomy in both sexes and in all leg pairs of the two species. The dendrites of the sensilla were oriented in a proximo-dorsal direction (Fig. 2). Some difference occurred between the two species in the number of sensilla, as the accessory organ in *G. immaculata* contained 7–12 sensilla, and in *G. helleri*, it contained 5–7 sensilla (Table 1). The slightly higher number in sensilla in *G. immaculata* occurred in all leg pairs. For *G. immaculata*, sufficient preparations were obtained for statistical analysis, and the differences in sensillum numbers for the three leg pairs were not statistically significant (one-way ANOVA: $p = 0.5063$, $F = 0.7031$, R squared = 0.06276; KS normality test: $p > 0.05$ for each leg pair).

Table 1. Numbers of sensilla in the accessory organ of two *Gonatoxia* species.

Species	Prothoracic leg	Mesothoracic leg	Metathoracic leg
G. immaculata	7–10	8–12	8–11
	(N = 9; n = 9)	(N = 9; n = 5)	(N = 6; n = 4)
G. helleri	6–7	5–7	7
	(N = 5; n = 5)	(N = 6; n = 5)	(n = 1)

The nerve pattern in the tibia was highly consistent between individuals. Some variation was seen only in one metathoracic leg, with the accessory organ and the single posterior campaniform sensillum having independent nerve branches instead of a shared nerve branch to the next-level branch from nerve N5B2 (female insect) (Fig. 4).

The subgenual organ with axons in nerve N5B2 had a ventral and a dorsal part (Figs 2, 3B–D). The complete subgenual organ in *G. immaculata* contained 41–55 sensilla.

Discussion

Among the Polyneoptera, the accessory organ is part of the subgenual organ complex in Blattodea (Schnorbus 1971), Mantophasmatodea (Eberhard et al. 2010), and in some groups of Ensifera. Among Tettigonioidea, it has been described in few species so far (Schwabe 1906, Strauß et al. 2016). These species included three members of Phaneropterinae: *Stilpnochlora couloniana* (Saussure, 1861), *Poecilimon mariannae* Willemse & Heller, 1992, and *Poecilimon ornatus* (Schmidt, 1850). Thus, the accessory organ occurs in different groups of Phaneropterinae and may even be a plesiomorphic trait of Tettigonioidea since it also occurs in the related Stenopelmatoidea and Rhaphidophoridae (Song et al. 2020).

Here, we document the neuroanatomy of the accessory organ in two *Gonatoxia* species. The accessory organ was found to be present in all leg pairs, with a similar nerve pattern found serially in all leg pairs. In the prothoracic leg, the nerve branches were more compressed in the proximo-distal direction compared to the mesothoracic and metathoracic legs. This is likely due to the enlarged acoustic trachea in the prothoracic leg associated with the tympanal hearing organ (Lakes and Schikorski 1990, Stumpner and Nowotny 2014).

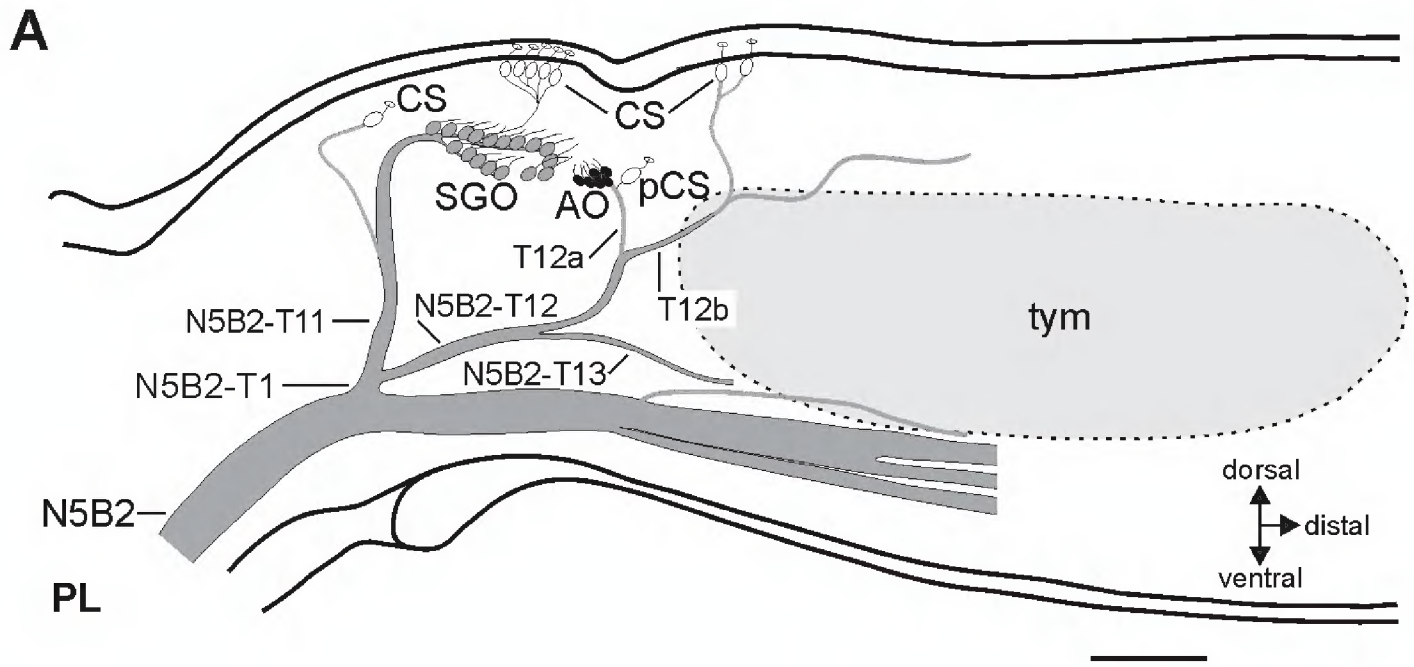

Fig. 2. Schematic of the nerve pattern of N5B2 in the proximal tibia in *G. immaculata* with the accessory organ, subgenual organ, and campaniform sensilla. The nerve branches and sensory elements are shown serially in the (**A**) prothoracic leg, (**B**) mesothoracic leg, and (**C**) metathoracic leg, lateral perspective. The accessory organ (AO) and subgenual organ (SGO) have separate nerve branches. Cell bodies from sensilla in the accessory organ are shown in black, cell bodies from the subgenual organ in grey, and cell bodies from the campaniform sensilla in white. N5B1 is not included in the schematic and is associated with further sensilla including the tympanal organ. Axes in all legs as indicated in **A**. All leg preparations are redrawn from legs of the same female insect. Abbreviations: AO, accessory organ; CS, campaniform sensilla; ML, mesothoracic leg; MTL, metathoracic leg; pCS, posterior campaniform sensillum; PL, prothoracic leg; SGO, subgenual organ; tym, tympanal membrane. Scale bars: 200 µm.

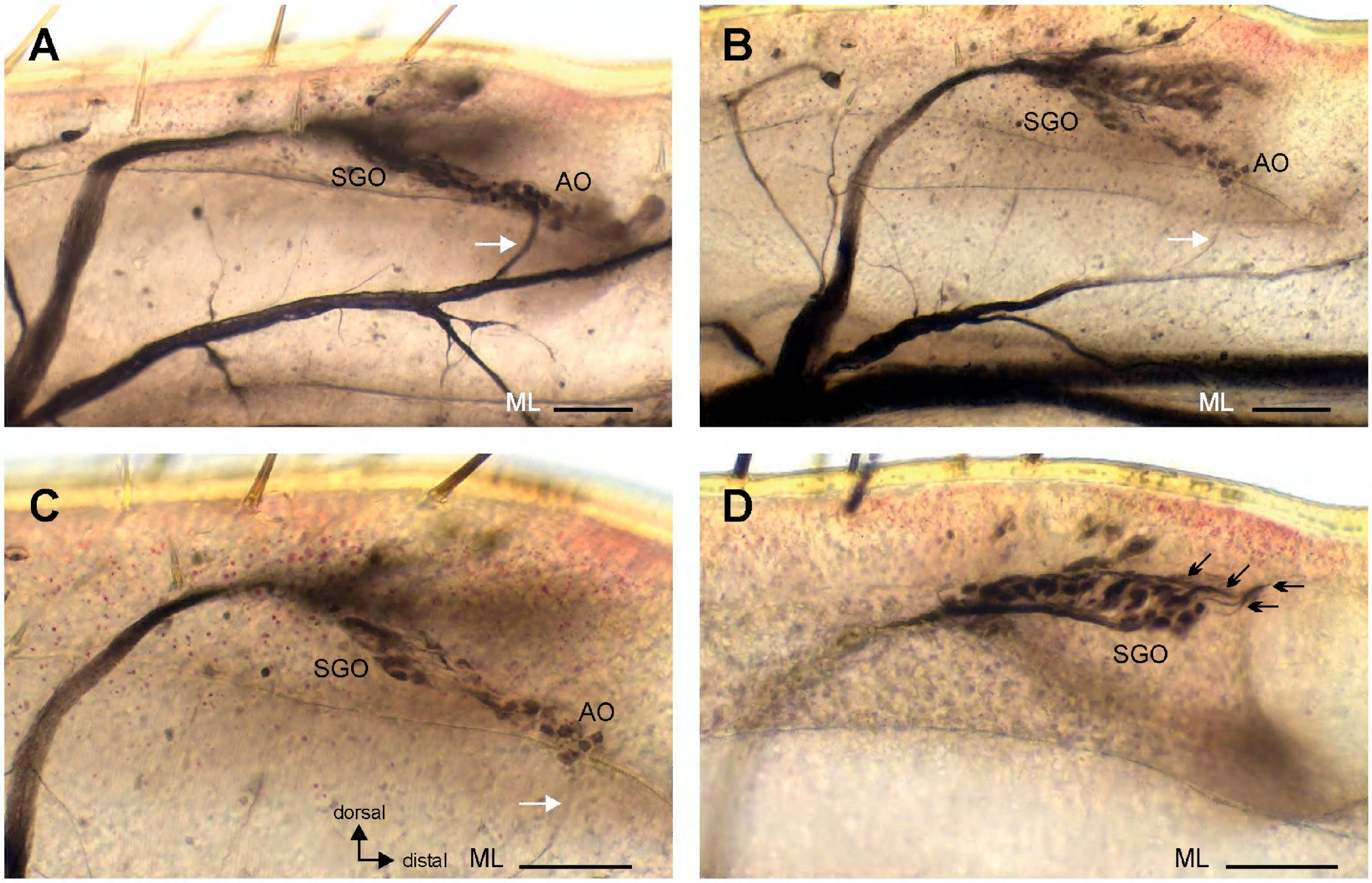

Fig. 3. Tracing preparations in the subgenual organ complex in *G. immaculata*. All preparations in lateral perspective, viewed from posterior. Axes as indicated in C. **A.** The accessory organ (AO) is placed next to the posterior sensilla of the subgenual organ (SGO). White arrow indicates the nerve branch associated with the AO. Preparation from a female insect. **B.** The SGO has a medial part (dorsally) and a posterior part (more ventrally), the latter is close to the AO. Separate planes are shown below for the posterior SGO (**C**) and the medial SGO (**D**). **C.** Plane of the same preparation as in C showing the AO and posterior SGO sensilla next to the AO. **D.** Plane of the same preparation as in C showing the sensilla of the medial SGO. Dendrites of the sensilla (black arrows) are pointing in distal direction. **B–D.** Preparation from a male insect. Abbreviations: AO, accessory organ; ML, mesothoracic leg; SGO, subgenual organ. Scale bars: 100 µm.

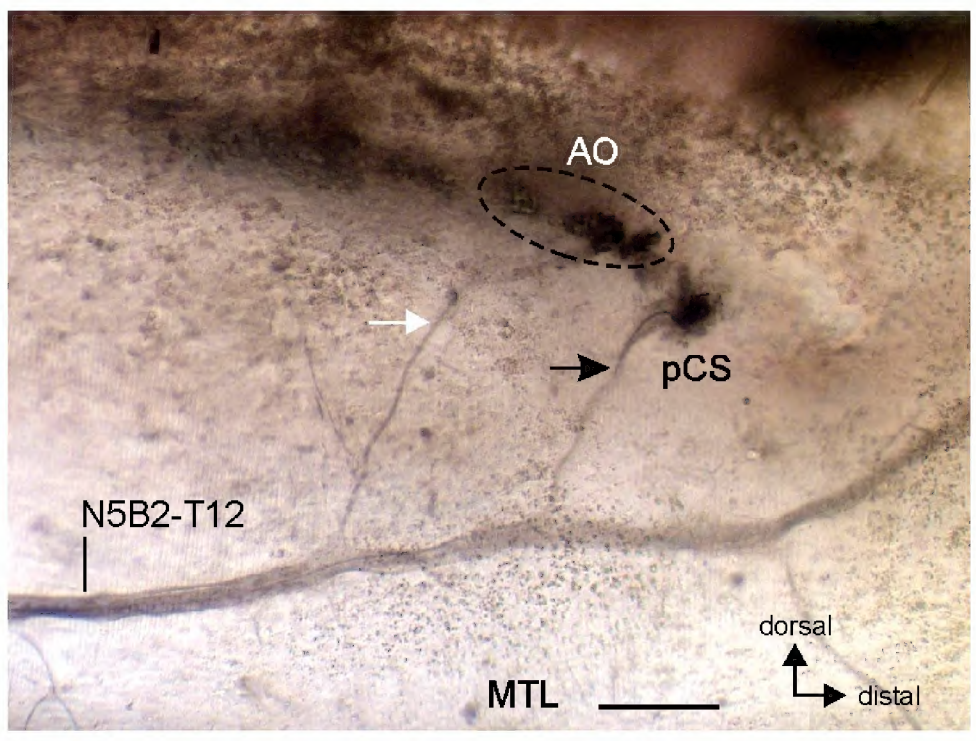

Fig. 4. Preparation with distinct nerve branches for the sensilla of the accessory organ (AO) (encircled), nerve branch indicated with white arrow, and the single posterior campaniform sensillum (pCS), nerve branch indicated with black arrow. Preparation from a female *G. immaculata* insect. Abbreviations: AO, accessory organ; MTL, metathoracic leg; pCS, posterior campaniform sensillum. Scale bar: 100 µm.

The overall neuroanatomy of the accessory organ resembles that documented in other tettigonioids. The number of scolopidial sensilla in the accessory organ in *G. immaculata* was slightly higher in all leg pairs than that in *G. helleri*. Both species are similar in body size (Hemp et al. 2016), making a putative scaling effect unlikely. It is unclear whether this relates to differences in physiological adaptations between the two species. During the analysis of phonotaxis and courtship, no body movements resembling tremulation-producing substrate vibrations were detected in *Gonatoxia* (K-GH, CH, unpublished observations). Since *G. helleri* is possibly the most recently evolved *Gonatoxia* species (Warchałowska-Śliwa et al. 2021), the lower number could indicate a regressive evolution leading to a lower number of sensilla in the accessory organ. Any possible change in vibrational stimuli relevant for behavior or in vibrational processing has yet to be identified.

The nerve pattern in the tibia is also similar to that of other tettigonioid species (Strauß et al. 2016). In particular, the accessory organ has a nerve branch separate from the subgenual organ. This nerve pattern is seen in other tettigonioid species with the notable exception of *Poecilimon ornatus*, in which the accessory organ is also placed next to the subgenual organ but the organs share the same nerve branch (Strauß et al. 2016). The finding of separate nerve branches in two species of Holochlorini shows a

broader distribution of these separate nerves in Phaneropterinae. Some differences in the overall nerve pattern of the tibia occur in the species from Phaneropterinae and Tettigoniinae studied before: The nerve branch to the subgenual organ is shared with the proximal campaniform sensillum (N5B2-T11), and an additional ventral nerve branch (N5B2-T13) merges with the nerve branch from the accessory organ. These differences in branching pattern result in a different numbering of homologous nerve branches (Strauß et al. 2016).

Thus far, the role of the accessory organ in vibration detection in Tettigonioidea has not been analyzed. It is known that certain bush-crickets produce acoustic signals in the form of tremulation signaling using substrate vibrations, as described in several species from the neotropical Conocephalinae and Pseudophyllinae (Stumpner et al. 2013, ter Hofstede et al. 2020, Korsunovskaya and Zhantiev 2022, Kernan et al. 2024) and the bradyporine *Ephippiger ephippiger* (Fiebig, 1784) (Keuper et al. 1985). Vibrational signaling in general is a signaling strategy against eavesdropping bats (Morris et al. 1994, Römer et al. 2010, ter Hofstede et al. 2017). Substrate vibrations caused by tegminal stridulation are also important in orientation of females towards signaling males in *Tettigonia cantans* (Fuessly, 1775) and *E. ephippiger* (Latimer and Schatral 1983, Stiedl and Kalmring 1989). Tremulation can also complement acoustic signals during courtship (Stritih-Peljhan et al. 2025), and when transmitted in woody vegetation, vibrations can also indicate the approach of potential competitors (Latimer and Schatral 1983). In addition to intraspecific communication, the detection of substrate vibrations can be important in predator detection (Cocroft and Rodríguez 2005, Virant-Doberlet et al. 2019), which is likely relevant in most tettigonioids, including *Gonatoxia*. While the subgenual organ commonly responds to a relatively broad frequency range of substrate vibrations (Stritih and Čokl 2014, Strauß et al. 2021), the accessory organ may also detect low-frequency vibrations, as it can in other Polyneoptera (Schnorbus 1971, Stritih-Peljhan et al. 2019). The occurrence and the physiological role of the accessory organ in tettigonioids, therefore, require further analysis for its contributions in sensory and behavioral physiology.

Author Contributions

Experiments: JS; data analysis: JS; figure assembly: JS, CH; writing manuscript (original draft): JS; writing manuscript (final script): JS, CH, K-GH; editing of the manuscript: JS, CH, K-GH; funding acquisition: CH. All authors read and edited the manuscript and agreed with the publication.

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Supplementary material 1

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Data type: xlsx
Explanation note: Numbers of scolopidial sensilla in the accessory organ (chordotonal organ) in two *Gonatoxia* species.
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